

Feeding patterns of Greenland halibut (*Reinhardtius hippoglossoides*) in Flemish Pass (Northwest Atlantic)

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Abstract

A qualitative study of the food composition of Greenland halibut (*Reinhardtius hippoglossoides*) was made by on-board analysis of commercially caught fish in 1992. The fish were caught east of Newfoundland (NAFO Div. 3LM) in unusually deep waters, with an average of 1 040 m. Variations in feeding according to predator size, depth and month were studied. The annual average percentage of empty stomachs was 69%, increasing through the year for specimens over 60 cm.

The frequency of occurrence (FO) of food items was used to evaluate the importance of prey groups. Fish (39%), cephalopods (32%) and decapod crustaceans (22%) were the main items, with cannibalism reaching 2%. An abrupt change in diet composition occurred in fish between 60 and 69 cm, from feeding on decapod crustaceans and cephalopods to fish and factory ship discarded offal. The influence of the fishery itself on the diet of Greenland halibut was observed when an important food component in the largest specimens (>60 cm) consisted of offal discarded after fish processing. This study indicates that the FO of the main prey groups bears more relation to the size of fish than with depth.

Key words: Depth, Flemish Pass, food, Greenland halibut

Introduction

Greenland halibut (*Reinhardtius hippoglossoides*) is one of the main demersal species in the NAFO area, representing 10–20% of the trawlable biomass estimated from annual Canadian bottom-trawl surveys in Div. 2J and 3K (Bowering and Lilly, 1992).

Since 1990 the Spanish fleet has been developing a new deep water fishery (800–2 000 m) in Flemish Pass, a deep channel situated between Eastern Newfoundland Grand Bank in NAFO Div. 3L and Flemish Cap in NAFO Div. 3M (Fig. 1), with Greenland halibut as the target species. The deepwater demersal fish in this area are exploited by Spanish, Portuguese fleets and vessels from

countries who are not members of NAFO. Greenland halibut catches for NAFO Subarea 3 have increased sharply in recent years due to the development of this fishery, and in the period 1985–89 average catches were 12 000 tons, increasing to 61 400 in 1992 (Bowering *et al.*, MS 1993)

The development of this fishery has provided the opportunity to study various aspects of the biology of Greenland halibut at unusual depths. The depth range of this species in the area is reported to be very wide (Bowering, MS 1984; Chumakov and Savvatimsky, 1990) reaching to 1 600 m (Templeman, 1973), but biological studies have been limited to a much narrower depth range (Smidt, 1969; Bowering and Brodie, 1991), usually not exceeding 800 m.

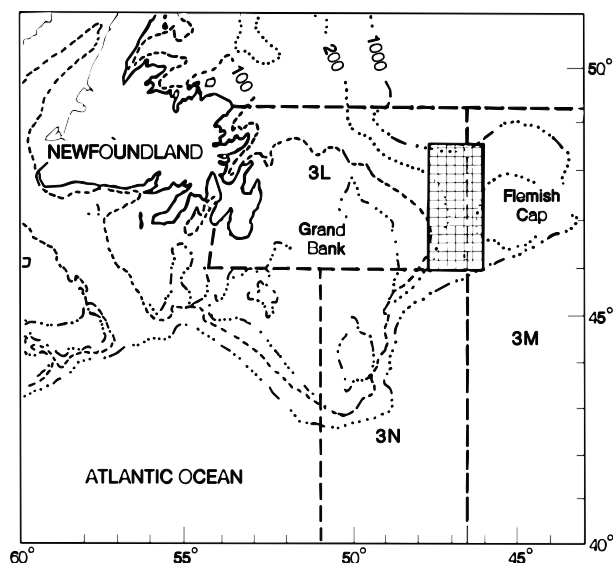


Fig. 1. Map of study area, (depth lines in fathoms).

In recent years several papers have been published on the feeding habits of Greenland halibut (Chumakov and Podrazhanskaya, 1986; Yang and Livingston, 1988; Bowering and Lilly, 1992; Pedersen and Riget, 1993), but the feeding patterns of this species at great depths remain fairly unknown. In this paper we provide a description of *R. hippoglossoides* feeding, taking into account seasonal and depth variations, influence of predator size, cannibalism and the influence of the fishery itself on the feeding patterns.

Materials and Methods

Sampling was carried out by observers on board commercial bottom trawl freezer ships in 1992. The study area was Flemish Pass, where the commercial fleet worked mainly in waters between 48°30'N and 46°N and 47°30'W and 46°W (Fig. 1), in depths ranging from 720 to 1 533 m, with an average depth of 1 040 m. A total of 242 200 specimens were examined from sampling through the whole year. Size and sex were determined for each specimen and stomach fullness was evaluated to determine the percentage of empty stomachs (%E).

For the analysis of stomach contents, separate sampling took place from May to November, and a total of 4 987 stomachs containing food were analyzed. In each haul a maximum of 100 Greenland halibut were randomly sampled. Size and sex were determined for each specimen. Stomach contents were analyzed on board. Classification of food components was limited to main taxonomic categories. The waste products discarded from factory ships after on-board fish processing, mainly heads

and tails of Greenland halibut, and heads, tails and alimentary tracts of grenadiers, were included in the category of offal, a term which refers to waste from the retained catch after gutting (Saila, 1983). From the total sampled, 168 stomachs were examined in detail and prey were identified to the lowest possible taxon. These stomachs were collected in May and June, at depths ranging from 730 to 909 m with an average of 815 m.

The frequency-of-occurrence method was used to characterize fish feeding, and only stomachs containing food were used for estimation (Dunn, 1954; Kennedy and Fitzmaurice, 1972). This method does not give quantitative information, but is quick and requires a minimum of apparatus, giving a somewhat qualitative picture of the food spectrum (Hyslop, 1980). The frequency-of-occurrence (percentage), (FO), is represented as:

$$FO = N_p/N_t \times 100$$

where N_p is the number of stomachs with a specific prey, and N_t is the total number of stomachs containing food.

For stomach content analysis, predator length, depth and month of the year were taken into account as follows: 8 predator length groups of 10 cm, 4 depth categories (<800, 800–999, 1 000–1 199, >1 199 m), and 7 months from May to November were considered. In Table 1a and Table 1b the number of stomachs for each group are shown.

Results

The average percentage of empty stomachs in 1992 was 69%, ranging from 62% in August to 84% in December. Considering size of fish in relation to seasonal variations in the year and depth (Fig. 2), it can be seen that the emptiness pattern varied very little with depth. There was an increasing trend of emptiness in summer and autumn, particularly for fish >50 cm, however in general, the percentage of empty stomachs diminished with size from 50 cm upwards. In Fig. 2, the tendency observed for specimens greater than 60 cm was different to that of specimens smaller than 60 cm; in the former, emptiness increased through the year, whereas in the latter an opposite pattern appeared, though less pronounced. This can be seen more clearly in Fig. 3 where the emptiness indices of both groups are compared. This Figure shows an increase in the percentage of empty stomachs through 1992 in specimens over 60 cm, reaching a maximum in the period from September to November, while in smaller specimens the emptiness index diminished reaching a minimum in the same period, the reverse process was apparent by December.

TABLE 1. Number of full stomachs analyzed: (a) by length range (cm) and month, and (b) by length range (cm) and depth (m).

| Month | (a) | | | | | | | | Total |
|-----------|-----|-------|-------|-------|-------|-------|-------|-----|-------|
| | <30 | 30–39 | 40–49 | 50–59 | 60–69 | 70–79 | 80–89 | >89 | |
| May | 0 | 56 | 368 | 277 | 136 | 60 | 20 | 12 | 929 |
| June | 0 | 26 | 146 | 216 | 110 | 39 | 25 | 10 | 572 |
| July | 0 | 45 | 278 | 213 | 117 | 54 | 15 | 6 | 728 |
| August | 6 | 117 | 359 | 183 | 71 | 15 | 1 | 0 | 752 |
| September | 12 | 229 | 466 | 182 | 42 | 3 | 0 | 0 | 934 |
| October | 1 | 73 | 209 | 152 | 32 | 8 | 5 | 0 | 480 |
| November | 0 | 60 | 253 | 204 | 60 | 15 | 0 | 0 | 592 |
| Total | 19 | 606 | 2 079 | 1 427 | 568 | 194 | 66 | 28 | 4 987 |

| Depth | (b) | | | | | | | | Total |
|-------------|-----|-------|-------|-------|-------|-------|-------|-----|-------|
| | <30 | 30–39 | 40–49 | 50–59 | 60–69 | 70–79 | 80–89 | >89 | |
| <800 | 2 | 304 | 728 | 280 | 31 | 1 | 0 | 0 | 1 346 |
| 800–999 | 14 | 247 | 959 | 657 | 228 | 60 | 15 | 2 | 2 182 |
| 1 000–1 199 | 3 | 52 | 354 | 451 | 271 | 101 | 33 | 12 | 1 277 |
| >1 199 | 0 | 3 | 38 | 39 | 38 | 32 | 18 | 14 | 182 |
| Total | 19 | 606 | 2 079 | 1 427 | 568 | 194 | 66 | 28 | 4 987 |

To evaluate the influence of offal on the percentage of empty stomachs, the percentage was recalculated excluding these products and is shown in Fig. 3 for specimens greater than and smaller than 60 cm, since it was upwards of this length that the greater occurrence of offal was found. A tendency of the emptiness percentage to increase towards the end of 1992 was observed, mainly from August, when offal practically disappeared from the diet.

From the total sampling in which classification of food components was limited to main taxonomic categories (Table 2), and from stomachs examined in detail (Table 3), the prey taxa spectrum in the diet of *R. hippoglossoides* was made up of nearly 35 representatives of different systematic groups. In the total sampling (Table 2) fish was the main prey group, with a frequency of occurrence of 39%, and within this group the families Macrouridae, Pleuronectidae, Gadidae and the species *Antimora rostrata* stood out. Natantian crustaceans (FO = 22%) and cephalopods (FO = 32%), made up another important part of diet. Offal from fish processing occurred frequently, FO = 10%. In the sampling carried out in spring, when a special effort was made to identify prey (Table 3), the most important species were the decapod crustaceans *Acantheephyra pelagica* and *Pasiphaea tarda*; the cephalopod *Illex illecebrosus*; the fish families Myctophidae and Macrouridae, and the fish species *Mallotus villosus* and *R. hippoglossoides*.

Diet composition in relation to length

Decapod crustaceans were the main food source for specimens smaller than 30 cm (Table 2,

Fig. 4), along with the molluscs, particularly cephalopods. The importance of both, crustaceans and cephalopods, gradually decreased in specimens of greater sizes. There were no decapods in the diets of Greenland halibut over 70 cm, while the cephalopods became exclusively octopods. Fish, mainly the families Macrouridae and Gadidae and the species *A. rostrata* and *R. hippoglossoides* became important in specimens greater than 40 cm. Fish importance increased to reach over 50% of the diet in large specimens. The same occurred with offal. The diet composition was size-related, with an abrupt change from feeding on crustaceans and molluscs to fish and offal at about 60–69 cm (Fig. 4).

In the sampling carried out in spring (Table 3), the same tendencies were observed in the large prey groups as those seen in the sampling conducted from May to November. The natantian crustaceans made up a significant proportion (FO = 26%) in the diet of specimens from 30 to 60 cm, Infraorder Caridea being particularly common. The importance of squids diminished as size increased, the opposite of which occurred for fish and offal. The consumption of grenadiers increased with size, and cannibalism occurred in specimens greater than 50 cm.

Diet composition in relation to season and length

In general, large seasonal differences were not observed in the diet of specimens smaller than 50 cm. Specimens of 30–50 cm fed mainly on cephalopod molluscs, although in August and November consumption of crustaceans increased, and

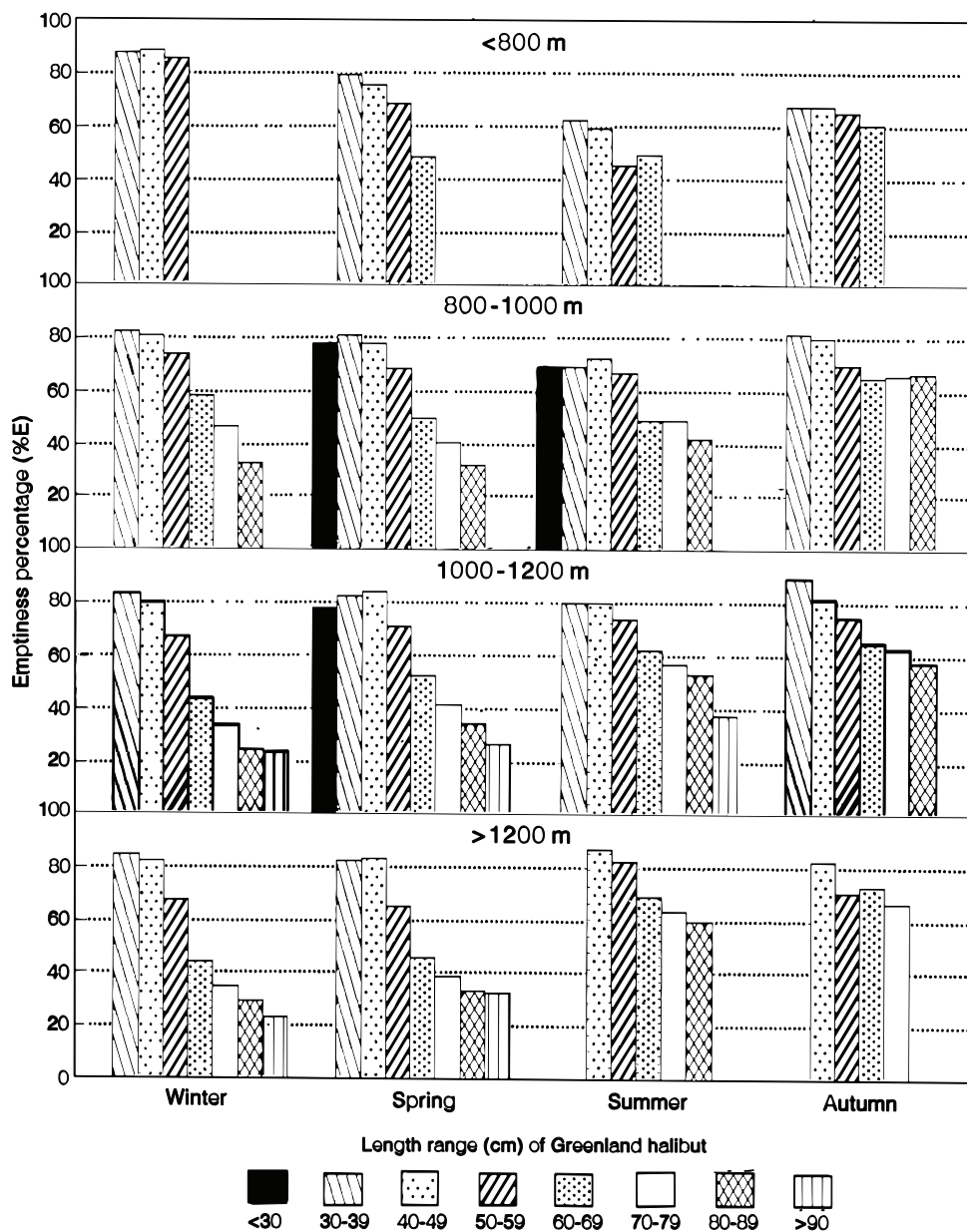


Fig. 2. Emptiness percentage (%E) of Greenland halibut in NAFO Div. 3LM, by length group, season and depth (minimum sample size = 50 stomachs).

that of fish decreased in July and November. In larger specimens, the frequency of occurrence of crustaceans, molluscs and fish was more important from August with a parallel decrease in the consumption of offal (Fig. 5). The average depths of hauls in different months did not vary greatly, which indicated that these tendencies were not due to this factor. The insufficient number of stomachs per month of specimens greater than 70 cm prevented the evaluation of differences between these and the rest of the length ranges.

Diet composition in relation to depth and length

As illustrated by the stomach contents of specimens by depth strata in Table 4, fish and offal were the main prey at greater depth, while crustaceans and molluscs were more important at shallower depths. If we take into account the frequency of occurrence of the most important prey groups with respect to size and depth at the same time (Fig. 6), it can be seen that depth did not greatly alter diet composition with respect to the large taxonomic groups and that size was the dominant factor. The

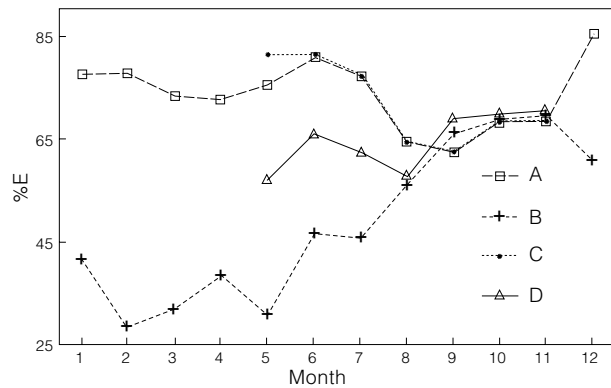


Fig. 3. Emptiness percentage (%E) through the year for specimens (A) smaller than 60 cm, (B) greater than 60 cm, (C) smaller than 60 cm adjusted to exclude offal and (D) greater than 60 cm adjusted to exclude offal.

discrepancy is due to the fact that as depth increases, the average length of specimens also increases (see average length by depth at the bottom of Table 4). This relationship has already been described by Junquera *et al.* (MS 1992) in the Flemish Pass area, and by Bowering (1982), Bowering and Chumakov (1989), for other areas.

Cannibalism

The rate of cannibalism was 1.7% (Table 2), increasing with length, to reach values greater than 15% in specimens larger than 80 cm. The predator length range was wide: 37–98 cm, and the prey range was from 13 to 46 cm. Of the 86 cases of cannibalism found, 78% were at lengths greater than 60 cm. The relationship between predator and prey length, was significant ($N = 26$, $P < 0.001$), although a determination coefficient (r^2) of 0.40 was obtained for the linear regression function (Fig. 7).

Discussion

Analyzing the Greenland halibut emptiness index by month in 1992, and taking this percentage as a measure of feeding intensity, there was a different pattern in feeding intensity among specimens greater than 60 cm to that of smaller ones (Fig. 3). It is upwards of 60 cm that maturity takes place, since the length range of female 50% maturity (M_{50}) obtained for the Flemish Pass area (Div. 3LM) varies between 67 and 73 cm (Junquera and Zamarro, MS 1992), which is similar to results obtained by Bowering (1983) for NAFO Subareas 0 and 2. Although we do not have data of M_{50} for males in Flemish Pass, in the Norwegian-Barents Sea, Kovtsova and Nizovtsev (MS 1985) found M_{50} to be lower for males than for females, confirming the different growth rate between sexes. Furthermore, Yatsu *et*

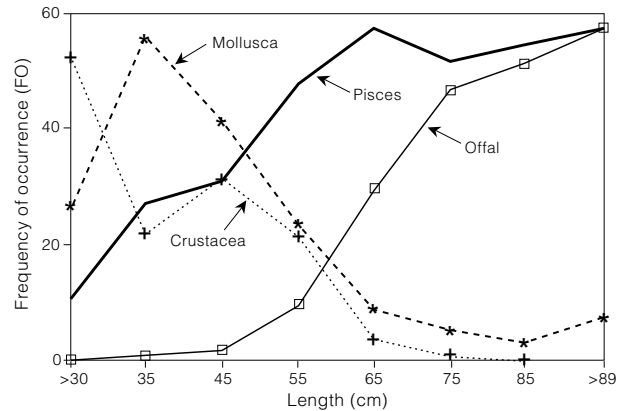


Fig. 4. Greenland halibut main diet components by length group (cm), expressed as frequency of occurrence (FO).

al. (MS 1988) observed that the gonad index (percentage of gonad weight against total body weight) in NAFO Div. 1CD increased from 4 in August to 12 in November and December; and Junquera (MS 1994) found a peak in the percentage of mature fish at the end of summer and beginning of autumn of 1992 for NAFO Div. 3LM. This appears to indicate that feeding intensity varies according to sexual maturity of Greenland halibut, between the reproducing stock and juveniles.

Chumakov and Podrazhanskaya (1986), found that the specimens sampled in NAFO Subarea 3, fed more intensively in summer and autumn than in winter and spring, which is similar to our results for specimens smaller than 60 cm. It is precisely this group which makes up the highest proportion of the catch, and which is mostly found at shallower depths. In fact, the feeding pattern found by Chumakov and Podrazhanskaya (1986) coincides with what we found for Greenland halibut caught at less than 800 m (Fig. 2), the depth at which these authors sampled.

We found that emptiness did not greatly vary with depth, except in summer, length being the most influential factor (Fig. 2). In the literature consulted, the depth range is much smaller than that of the present study, Bowering and Lilly (1992) found that the percentage of emptiness increased from the stratum 601–800 to 801–1 000 m in autumn, coinciding with our results for the same season and depth range, and it was from 800 m that we found that emptiness remained constant. Chumakov and Podrazhanskaya (1986) also found an increase in feeding intensity with depth (strata <500 m and >500 m). It is proposed that variations in feeding intensity with depth must take length into account,

TABLE 2. Prey items found in Greenland halibut stomachs sampled from May to November 1992, expressed as frequency of occurrence by length group (cm), + indicates presence but percentage <0.5.

| Prey taxa/length (cm) | <30 | 30-39 | 40-49 | 50-59 | 60-69 | 70-79 | 80-89 | >89 | Total |
|-------------------------------------|------|-------|-------|-------|-------|-------|-------|------|-------|
| CRUSTACEA | | | | | | | | | |
| Other Crustacea | | | + | + | | | | | + |
| Decapoda | | | | | | | | | |
| Natantia | 52.6 | 21.6 | 31.4 | 21.4 | 3.7 | 0.5 | | | 22.5 |
| Total CRUSTACEA | 52.6 | 21.6 | 31.3 | 21.4 | 3.7 | 0.5 | | | 22.5 |
| MOLLUSCA | | | | | | | | | |
| Gastropoda | | | | + | | | | | + |
| Cephalopoda | | | | | | | | | |
| Decapoda | | 7.8 | 10.6 | 4.3 | 1.2 | 2.1 | | | 6.8 |
| Octopoda | | | | + | | 1.0 | 3.0 | 3.6 | + |
| Unidentified Cephalopoda | 26.3 | 47.9 | 30.6 | 18.0 | 7.0 | 2.1 | | | 24.7 |
| Unidentified Mollusca | | + | + | + | + | | | 3.6 | + |
| Total MOLLUSCA | 26.3 | 55.8 | 41.4 | 23.0 | 8.6 | 5.2 | 3.0 | 7.1 | 32.0 |
| OTHERS INVERTEBRATES | | | | | | | | | |
| Cnidaria | | | + | | | | | | + |
| Polychaeta | | | + | | | | | | + |
| Total O. INVERTEBRATES | | + | + | | | | | | + |
| OTHERS | | | | | | | | | |
| Unidentified | 10.5 | 0.5 | 2.5 | 6.0 | 9.5 | 7.2 | 4.6 | 7.1 | 4.3 |
| Stones | | | | | | | 1.5 | | + |
| Offal | | 0.5 | 1.7 | 9.4 | 29.0 | 46.9 | 51.5 | 57.1 | 9.6 |
| Total OTHERS | 10.5 | 1.0 | 4.2 | 15.0 | 37.7 | 51.6 | 54.6 | 60.7 | 13.6 |
| PISCES | | | | | | | | | |
| Gadidae | | | | | | | | | |
| <i>Gadus morhua</i> | | | + | + | | | | | + |
| <i>Gaidropsarus</i> sp. | | | + | 0.9 | 1.2 | 0.5 | 3.0 | | 0.5 |
| <i>Urophycis</i> sp. | | | + | + | 1.1 | 3.1 | 3.0 | 3.6 | + |
| Total Gadidae | | | + | 1.3 | 2.3 | 3.6 | 6.1 | 3.6 | 1.0 |
| Macrouridae | | | | | | | | | |
| <i>Coryphaenoides rupestris</i> | | + | + | 2.7 | 5.8 | 5.7 | 7.6 | 3.6 | 1.9 |
| <i>Macrourus berglax</i> | | | 0.6 | 1.5 | 2.6 | 2.1 | 1.5 | | 1.1 |
| <i>Nezumia bairdi</i> | | + | 1.2 | 4.1 | 3.5 | 2.6 | 1.5 | | 2.2 |
| Unidentified Macrouridae | | + | 1.2 | 3.7 | 5.3 | 4.1 | 6.1 | 3.6 | 2.5 |
| Total Macrouridae | | 0.5 | 3.2 | 11.8 | 17.3 | 14.4 | 15.2 | 7.1 | 7.6 |
| Moridae | | | | | | | | | |
| <i>Antimora rostrata</i> | | | + | 2.4 | 4.4 | 3.6 | 4.6 | 7.1 | 1.6 |
| Notacanthidae | | | | | | | | | |
| <i>Notacanthus chemnitzii</i> | | | | | + | | | 3.6 | + |
| Anarhichadidae | | | | | | | | | |
| <i>Anarhichas</i> sp. | | | | + | + | | | | + |
| Scorpaenidae | | | | | | | | | |
| <i>Sebastes</i> sp. | | | + | + | + | 1.6 | 1.5 | | + |
| Zoarcidae | | | | | | | | | |
| <i>Lycodes</i> sp. | | | | | + | 1.6 | | | + |
| Pleuronectidae | | | | | | | | | |
| <i>Hippoglossoides platessoides</i> | | | | | + | | | | + |
| <i>Reinhardtius hippoglossoides</i> | | + | + | 1.2 | 5.6 | 8.8 | 15.2 | 25.0 | 1.7 |
| Total Pleuronectidae | | + | + | 1.2 | 5.8 | 8.8 | 15.2 | 25.0 | 1.7 |
| Pisces | | | | | | | | | |
| Others + Unidentified | 10.5 | 26.2 | 26.6 | 31.0 | 28.5 | 21.7 | 15.2 | 17.9 | 27.6 |
| Other Squaliformes | | | | | | 1.5 | | + | |
| Other Rajidae | | | + | | | | | + | |
| Total PISCES | 10.5 | 26.9 | 30.6 | 47.6 | 57.4 | 51.6 | 54.6 | 57.1 | 39.4 |
| No. STOMACHS: | 19 | 606 | 2 079 | 1 427 | 568 | 194 | 66 | 28 | 4 987 |
| MEAN LENGTH: | 26 | 36 | 45 | 54 | 64 | 74 | 83 | 94 | 50 |

TABLE 3. Prey items found in Greenland halibut stomachs in spring 1992, expressed as frequency of occurrence by length group (cm), + indicates presence but percentage <0.5.

| Prey taxa/length | 30–39 | 40–49 | 50–59 | 60–69 | Total |
|-------------------------------------|-------|-------|-------|-------|-------|
| CRUSTACEA | | | | | |
| Other Crustacea | | 1.1 | 2.6 | | 1.2 |
| Decapoda | | | | | |
| Aristeidae | | | | | |
| <i>Plesiopenaeus edwardsianus</i> | | 3.3 | | | 1.8 |
| Oplophoridae | | | | | |
| <i>Acanthephyra pelagica</i> | 10.5 | 12.1 | 12.8 | | 11.3 |
| Pasiphaeidae | | | | | |
| <i>Pasiphaea tarda</i> | 10.3 | 18.7 | 5.1 | | 13.1 |
| Total CRUSTACEA | 20.7 | 33.0 | 20.5 | | 26.2 |
| MOLLUSCA | | | | | |
| Bivalvia | | 1.1 | | | 0.6 |
| Cephalopoda | | | | | |
| Unidentified Cephalopoda | 17.2 | 13.2 | 2.6 | | 10.7 |
| Decapoda | | | | | |
| <i>Illex illecebrosus</i> | 24.1 | 14.3 | 2.6 | | 12.5 |
| Total MOLLUSCA | 41.4 | 27.5 | 5.1 | | 23.2 |
| OTHERS | | | | | |
| Offal | 6.9 | 12.1 | 25.6 | 44.4 | 16.1 |
| PISCES | | | | | |
| Serrivomeridae | | | | | |
| <i>Serrivomer beani</i> | | | 2.6 | | 0.6 |
| Synphobranchidae | | | | | |
| <i>Synphobranchus kaupi</i> | | | 5.1 | | 1.2 |
| Gadidae | | | | | |
| <i>Gadus morhua</i> | | 1.1 | 2.6 | | 1.2 |
| Macrouridae | | | | | |
| <i>Macrourus berglax</i> | | 3.3 | 5.1 | | 3.0 |
| <i>Nezumia bairdi</i> | | 1.1 | 2.6 | 11.1 | 1.8 |
| Unidentified Macrouridae | | | 5.1 | 11.1 | 1.8 |
| Total Macrouridae | | 4.4 | 12.8 | 22.2 | 6.6 |
| Moridae | | | | | |
| <i>Antimora rostrata</i> | | | 5.1 | | 1.2 |
| Myctophidae | | | | | |
| Myctophidae | 10.3 | 9.9 | 5.1 | 11.1 | 8.9 |
| Pisces | | | | | |
| Pisces unidentified | 10.3 | 11.0 | 10.4 | 11.1 | 10.7 |
| Pleuronectidae | | | | | |
| <i>Reinhardtius hippoglossoides</i> | | | 7.7 | 11.1 | 3.0 |
| Chauliodontidae | | | | | |
| <i>Chauliodus sloani</i> | | 1.1 | | | 0.6 |
| Osmeridae | | | | | |
| <i>Mallotus villosus</i> | 6.9 | 4.4 | | | 3.6 |
| Rajidae | | | | | |
| <i>Raja radiata</i> | | 1.1 | | | 0.6 |
| Total PISCES | 31.0 | 33.0 | 51.8 | 55.6 | 38.1 |
| No. STOMACHS: | 29 | 91 | 39 | 9 | 168 |
| MEAN LENGTH: | 37 | 45 | 54 | 62 | 47 |

given that from our work the emptiness index diminished as length increased, coinciding with the results obtained by Yang and Livingston (1988).

Fish are processed on the Spanish commercial vessels, producing a variety of waste products,

which are thrown overboard. These appear in stomach contents, being easily identifiable by the cuts produced by the processing machine and by their appearance in the form of isolated structures. These offal are largely consumed by large specimens found at greater depth. Offal are an extra provision

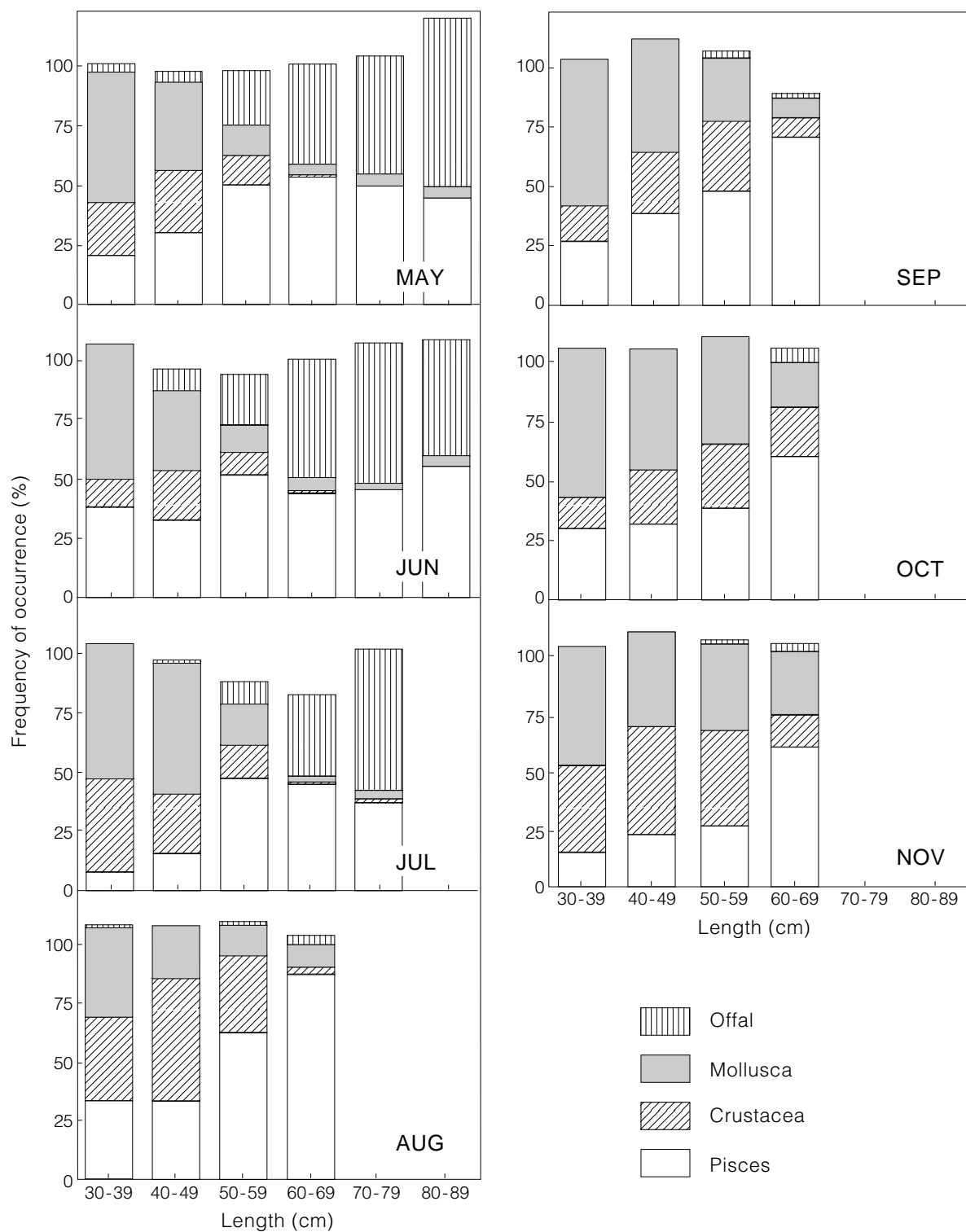


Fig. 5. Greenland halibut main diet components by length group (cm) and month.

of food introduced by fishing activity. This is a new component in the diet, which represented a high mean occurrence percentage, FO = 10%, and

reached values higher than 45% in specimens larger than 70 cm. These high percentages show the opportunistic feeding character of this species.

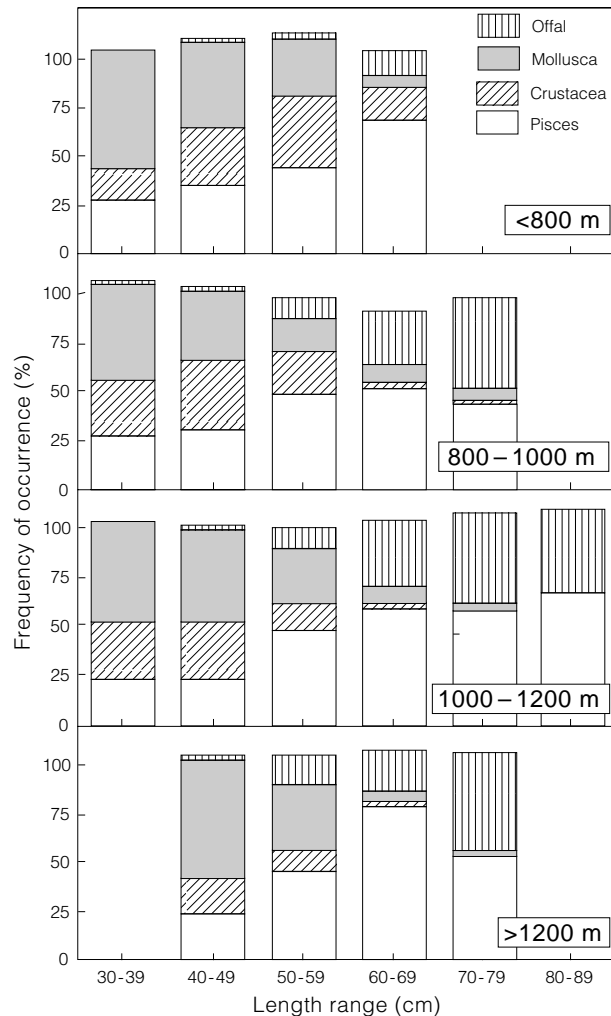


Fig. 6. Greenland halibut main diet components by length group (cm) and depth.

Stomachs containing offal influenced the percentages of the rest of the diet components and emptiness. They are difficult, in fact, to interpret, since offal is not “natural food” and such stomachs can be considered neither empty nor full. In other words not all stomachs containing offal would have contained “natural food”, but undoubtedly nor would they have all been empty. In Fig. 3, by representing the percentage of empty stomachs adjusted to exclude offal, we artificially increased the number of empty stomachs, and even though the stomach sampling did not cover the whole year, the tendency remained for the number of empty stomachs to increase through the year, the months of greater emptiness being those where offal were practically absent. The frequency of occurrence of offal registered a fall from May to November, mainly from August (Fig. 5). These variations could be due to the extent to which the fleet concentrates on certain fishing areas in certain months and the fact that the

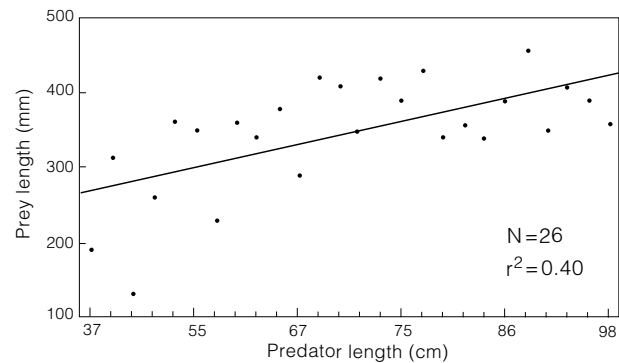


Fig. 7. Regression line between predator length and prey length (Cannibalism).

number of specimens larger than 70 cm sampled from August onwards was minimal, these being the main consumers of waste products (no relationship was found between the presence of offal in stomachs and the catch of Greenland halibut and grenadiers, nor with fishing effort).

The abundance of pelagic and bathypelagic species present in the diet of *R. hippoglossoides* shows that this species leaves the bottom to feed (Smidt, 1969; Chumakov and Podrazhanskaya, 1986; Yang and Livingston, 1988; Albikovskaya *et al.*, MS 1988). Some of its morphological characteristics, such as the pigmentation on both sides of the body and the apical position of the left eye (De Groot, 1970), indicate its active movement in the water column. The presence of high percentages of natantian crustaceans and cephalopods in the diet of specimens smaller than 60 cm, suggests that the smaller Greenland halibut feed in the upper water column, while the larger fish (>60 cm) feed mainly on benthopelagic fish (term defined by Cage, 1991) such as Macrouridae, Pleuronectidae and *A. rostrata*, which in turn suggests a greater relationship with the overlying water column associated with the bottom. A similar pattern, though with different prey groups, was found by Yang and Livingston (1988) in the Eastern Bering Sea.

Greenland halibut is a fundamentally ichthyophagous species (Yang and Livingston, 1988; Bowering and Lilly, 1992), although in small specimens, decapod crustaceans and cephalopods (mainly squid) form an important part of their diet (Fig. 4). It is precisely in the frequency of occurrence of this latter prey group that the present work differs from the literature, since cephalopods have been reported as having low occurrence. This disparity in diet may be related to depth, as the consumption of prey organisms is intimately associated with their distribution and the bathypelagic way of life of Greenland halibut (Chumakov and

TABLE 4. Prey items found in Greenland halibut stomachs sampled from May to November 1992, expressed as frequency of occurrence by depth group (m), + indicates presence but percentage <0.5.

| Prey taxa/depth | <800 | 800-999 | 1 000-1 199 | >1 199 | Total |
|-------------------------------------|-------|---------|-------------|--------|-------|
| CRUSTACEA | | | | | |
| Other Crustacea | + | + | | 7.1 | + |
| Decapoda Natantia | 25.8 | 25.7 | 14.6 | | 22.5 |
| Total CRUSTACEA | 26.8 | 25.6 | 14.6 | 7.1 | 22.5 |
| MOLLUSCA | | | | | |
| Gastropoda | + | + | + | | + |
| Cephalopoda | | | | | |
| Decapoda | 1.2 | 9.2 | 8.9 | 5.5 | 6.8 |
| Octopoda | | + | + | 2.2 | + |
| Unidentified Cephalopoda | 43.2 | 18.1 | 17.6 | 16.5 | 24.7 |
| Unidentified Mollusca | | + | + | + | + |
| Total MOLLUSCA | 44.5 | 27.6 | 27.3 | 24.7 | 32.0 |
| OTHER INVERTEBRATES | | | | | |
| Cnidaria | | + | | | + |
| Polychaeta | + | | | | + |
| Total O. INVERTEBRATES | + | + | | | + |
| OTHERS | | | | | |
| Unidentified | 1.0 | 5.7 | 5.8 | 2.2 | 4.3 |
| Stones | | | | 0.6 | + |
| Offal | 1.4 | 8.9 | 16.7 | 28.0 | 9.6 |
| Total OTHERS | 2.3 | 14.4 | 21.7 | 29.7 | 13.6 |
| PISCES | | | | | |
| Gadidae | | | | | |
| <i>Gadus morhua</i> | + | + | | | + |
| <i>Gaidropsarus</i> sp. | + | 0.8 | 0.6 | | 0.5 |
| <i>Urophycis</i> sp. | | + | 0.6 | 6.0 | + |
| Total Gadidae | + | 1.0 | 1.1 | 6.0 | 1.0 |
| Macrouridae | | | | | |
| <i>Coryphaenoides rupestris</i> | + | 0.7 | 4.2 | 13.7 | 1.9 |
| <i>Macrourus berglax</i> | + | 1.1 | 1.8 | 0.6 | 1.1 |
| <i>Nezumia bairdi</i> | 1.0 | 3.0 | 2.0 | 1.7 | 2.2 |
| Unidentified Macrouridae | 0.5 | 3.2 | 3.3 | 2.2 | 2.5 |
| Total Macrouridae | 2.2 | 7.9 | 11.1 | 18.1 | 7.6 |
| Moridae | | | | | |
| <i>Antimora rostrata</i> | + | 1.3 | 3.7 | 2.8 | 1.6 |
| Notacanthidae | | | | | |
| <i>Notacanthus chemnitzii</i> | | + | + | | + |
| Anarhichadidae | | | | | |
| <i>Anarhichas</i> sp. | | + | | 0.6 | + |
| Scorpaenidae | | | | | |
| <i>Sebastes</i> sp. | + | + | + | 1.1 | + |
| Zoarcidae | | | | | |
| <i>Lycodes</i> sp. | | + | + | 1.1 | + |
| Pleuronectidae | | | | | |
| <i>Hippoglossoides platessoides</i> | | + | | | + |
| <i>Reinhardtius hippoglossoides</i> | + | 0.8 | 4.0 | 7.1 | 1.7 |
| Total Pleuronectidae | + | 0.9 | 4.0 | 7.1 | 1.7 |
| Pisces | | | | | |
| Others + Unidentified | 33.0 | 27.3 | 23.7 | 17.6 | 27.6 |
| Other Squaliformes | | | | 0.6 | + |
| Other Rajidae | | + | | | + |
| Total PISCES | 35.6 | 38.6 | 42.9 | 50.6 | 39.4 |
| No. STOMACHS: | 1 346 | 2 182 | 1 277 | 182 | 4 987 |
| MEAN LENGTH: | 45 | 49 | 56 | 64 | 50 |

Podrazhanskaya, 1986). It would seem that at great depths (700–1 200 m) squid play a similar role in the diet of Greenland halibut to that of capelin on the continental shelf, given that their maximum occurrence appeared in predators smaller than 60 cm and disappeared from the diet of larger specimens. From 60 cm an abrupt diet change took place, and fish and offal became dominant (Fig. 4).

From our results, diet did not vary considerably with depth in terms of large taxonomic groups, with the exception of crustaceans whose frequency of occurrence diminished as specimens of the same length group were found at greater depth. This indicates that diet is more size related than depth related, although composition by species undoubtedly has to vary with depth, as Chumakov and Podrazhanskaya (1986) affirm. Whichever the case may be, in Table 4 a higher presence of species like *Macrourus berglax*, *Nezumia bairdi*, *Coryphaenoides rupestris* and *A. rostrata* was recorded in the diet of Greenland halibut as depth increased. The range of bathymetric distribution of these species (Savvatimsky, 1989a; 1989b; MS 1992; Wenner and Musick, 1977) makes them ideal prey for large sized Greenland halibut.

The cannibalism rate increases, in general, with predator size, and so, its value will bear relation to the length distribution of the sample. This makes the comparison between studies with different percentages of large specimens difficult. In the present study 78% of the cases of cannibalism were found in specimens larger than 60 cm. Despite this fact the rate found was intermediate, FO = 0.54% (empty stomachs considered), between that calculated by Chumakov and Podrazhanskaya (1986), FO = 0.3%, for NAFO Subarea 3, and the averages obtained by Pedersen and Riget (1993), FO = 1% for NAFO Subarea 1, and by Bowering and Lilly (1992), FO = 1.37% for NAFO Div. 2J3K, although the latter authors did not find cannibalism in the stratum 801–1 000 m.

No clear seasonal feeding trends were found, and a more accurate analysis of prey identification is needed to establish differences in the diet with season and depth. Continued annual sampling is also needed to be able to confirm our results, which indicate that on the continental slope at depths over 800 m, the cephalopods and grenadiers are of greater importance in the trophic chain than has been previously considered in the general descriptions of the Greenland halibut diet.

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